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Ecosystem effects of CO₂ concentration: evidence from past climates

I. C. Prentice¹ and S. P. Harrison²

¹QUEST, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Bristol BS8 1RJ, UK

²School of Geographical Sciences, University of Bristol, University Road, Bristol BS8 1SS, UK

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Abstract. Atmospheric CO₂ concentration has varied from minima of 170–200 ppm in glacials to maxima of 280–300 ppm in the recent interglacials. Photosynthesis by C₃ plants is highly sensitive to CO₂ concentration variations in this range. Physiological consequences of the CO₂ changes should therefore be discernible in palaeodata. Several lines of evidence support this expectation. Reduced terrestrial carbon storage during glacials, indicated by the shift in stable isotope composition of dissolved inorganic carbon in the ocean, cannot be explained by climate or sea-level changes. It is however consistent with predictions of current process-based models that propagate known physiological CO₂ effects into net primary production at the ecosystem scale. Restricted forest cover during glacial periods, indicated by pollen assemblages dominated by non-arboreal taxa, cannot be reproduced accurately by palaeoclimate models unless CO₂ effects on C₃–C₄ plant competition are also modelled. It follows that methods to reconstruct climate from palaeodata should account for CO₂ concentration changes. When they do so, they yield results more consistent with palaeoclimate models. In conclusion, the palaeorecord of the Late Quaternary, interpreted with the help of climate and ecosystem models, provides evidence that CO₂ effects at the ecosystem scale are neither trivial nor transient.

Lüthi et al., 2008). Atmospheric CO₂ concentration (c_a) is a limiting factor for the photosynthesis of C₃ plants even at today's elevated values (>380 ppm), and was much more strongly limiting at glacial values (Polley et al., 1993, 1995; Beerling and Woodward, 1993; Cowling and Sage, 1998; Guiot et al., 2001). Free Air Carbon dioxide Enrichment (FACE) experiments have shown that an increase of c_a by 200 ppm increases net primary production (NPP) in temperate forests by 23±2% (Norby et al., 2005). The response of photosynthesis to CO₂ in C₃ plants is a consequence of both substrate (CO₂) limitation and competition from O₂ at the reaction site on Rubisco, the enzyme responsible for CO₂ fixation. Plants using the C₄ photosynthetic pathway are less strongly influenced by c_a because they are anatomically and physiologically adapted to low c_a , using mechanisms that concentrate CO₂ near the chloroplasts. Because CO₂ concentration affects C₃ photosynthesis, and must indirectly influence the competition between C₃ and C₄ plants (e.g. between C₃ trees and C₄ grasses in tropical savannas), it makes sense to look for CO₂ effects that might be superimposed on climate change effects in palaeoecological records. Moreover, if these variations in c_a have caused changes that are detectable in compositional data, such as pollen assemblages, then conventional approaches to reconstructing past climate using statistical or analogue methods – if applied to periods with c_a different from that of the late Holocene – are certain to yield incorrect results. Although this potential problem in palaeoclimate reconstruction has been known in principle for more than two decades (Solomon, 1984; Idso, 1989; Farquhar, 1997; Street-Perrott, 1994; Street-Perrott et al., 1997; Cowling and Sykes, 1999, 2000; Bennett and Willis, 2000; Williams et al., 2000; Loehle, 2007), until recently few systematic attempts have been made to rectify it.

The relative neglect of CO₂ effects in Quaternary palaeoecology may have been encouraged by an influential school of thought in contemporary biogeochemistry, which questions the relevance of plant-physiological effects of CO₂ over the

1 Introduction

Atmospheric CO₂ concentration has varied in a quasi-cyclical manner from minima of 170–200 ppm in glacials to maxima of 280–300 ppm in the recent “warm” interglacials, varying predictably with Antarctic temperature variations through the past 0.8 million years (Siegenthaler et al., 2005;



Correspondence to: I. C. Prentice
(colin.prentice@bristol.ac.uk)

long term and at the ecosystem scale (e.g. Körner, 2000). A much-debated hypothesis suggests, in particular, that limitations in the supply of nitrogen needed to support increased plant growth should over time reduce or eliminate any effect of c_a on NPP (Luo et al., 2004). However, clear evidence in support of this “progressive nitrogen limitation” (PNL) hypothesis has not emerged to date (see e.g. Moore et al., 2006). Equivocal results from a single FACE experiment in a mature forest have been interpreted as indicating a limited or non-existent CO₂ fertilization effect in mature forests generally (Körner et al., 2005; see Norby et al., 2005 for a critique). Interpretations of experimental data have tended to emphasize the influence of N limitation on the CO₂ effect (e.g. Nowak et al., 2004). Nevertheless, it is well established that elevated CO₂ can increase NPP, even in ecosystems where N supply is demonstrably limiting to plant growth (e.g. Lloyd and Farquhar 1996, 2000; Nowak et al., 2004). There is some evidence that plants can increase their N supply to support CO₂-enhanced growth, perhaps by increased root penetration or increased labile carbon subsidy to the rhizosphere (Finzi et al., 2007). The extent to which ecosystems can respond to CO₂ enhancement over timescales longer than a decade has not been unambiguously demonstrated by experiments, and is subject to our still incomplete quantitative understanding of the mechanisms of N acquisition by plants.

Controversy thrives in this field in part because the evidence base from contemporary studies is, inevitably, limited. FACE has provided a great deal of extremely valuable information, and remains the key experimental technology needed to unravel CO₂ effects in intact ecosystems. However, FACE experiments are expensive and technically challenging, especially in forests. No feasible experiment can test the multi-decadal responses of ecosystems and biomes on a large spatial scale. In this paper, we show that long-term, ecosystem- and biome-level effects of CO₂ effects on plant physiology can be inferred from the palaeorecord. We argue that CO₂ effects are fundamental in establishing consistency between palaeovegetation data and palaeoclimate models.

2 Background

The concentration of CO₂ in the substomatal cavity, or “internal” CO₂ concentration (c_i), is a key quantity for photosynthesis in C₃ plants. The internal concentration in illuminated leaves is less than the ambient concentration, because photosynthesis draws down CO₂ while the stomata present a resistance to the inward diffusion of CO₂. The relationship between photosynthesis and the CO₂ concentration gradient across the leaf epidermis is represented by the diffusion equation,

$$A = g(c_a - c_i) \quad (1)$$

where A is the net rate of carbon assimilation and g is the stomatal conductance (the reciprocal of resistance) to CO₂.

Stomatal conductance is regulated in a way that maintains the c_i/c_a ratio typically around 0.7–0.8 in C₃ plants and 0.3–0.4 in C₄ plants under conditions of moderate vapour pressure deficit (vpd) and adequate soil moisture (Wong et al., 1979). Diffusion through the stomata also controls plant water loss:

$$E = 1.6gD \quad (2)$$

where E is the rate of transpiration per unit leaf area, and D is the vpd at the leaf surface. As D increases, g declines; in consequence, under conditions of increasing D , c_i/c_a is reduced while E increases towards a maximum (Monteith, 1995).

Equation (1) describes the control of c_i by A . At the same time, A is controlled by c_i , according to the following equation which summarizes the biochemical controls of photosynthesis (Farquhar et al., 1980: simplified here for expository purposes):

$$A = \min(A_c, A_j) - R_d \quad (3)$$

where:

$$A_c = V_{c\max}(c_i - \Gamma)/(c_i + K),$$

$$A_j = \phi_o I (c_i - \Gamma)/(c_i + 2\Gamma),$$

$$R_d = bV_{c\max}.$$

Here A_c is the Rubisco-limited photosynthetic rate, $V_{c\max}$ is a maximum rate (dependent on the activity of Rubisco), Γ is the CO₂ compensation point (the concentration at which photosynthesis is zero), and K is an effective Michaelis-Menten coefficient (dependent on O₂ concentration, but this has not varied significantly over the time scales considered here). A_j is the light-limited photosynthetic rate, ϕ_o is the intrinsic quantum efficiency of photosynthesis, and I is the absorbed flux of photosynthetically active radiation (PAR). R_d is the respiration rate required to maintain the activity of Rubisco and other photosynthetic enzymes; b is a small constant, representing a respiratory loss of 1–2% of $V_{c\max}$.

Leaves typically operate with values of $V_{c\max}$ such that typical daytime values of A_c and A_j are similar, i.e. there is approximate co-limitation by Rubisco and PAR (Farquhar et al., 1980). Co-limitation yields the optimum assimilation rate, because a lower $V_{c\max}$ would result in reduced utilization of available PAR while a higher $V_{c\max}$ would increase the loss of carbon in maintenance respiration for no gain in photosynthesis (e.g. Haxeltine and Prentice, 1996a). In practice, with light and other environmental conditions varying over the diurnal cycle, photosynthesis can be limited by Rubisco at some times and by PAR at others. However, both rates are characterized by a response to c_i that increases most steeply just above $c_i = \Gamma$, and approaches an asymptote at high c_i . Thus, the response of A to c_a is steepest at low

c_a and approaches saturation at high c_a . If $V_{c\max}$ is optimal, increased c_a should lead to reduced $V_{c\max}$ (this “down-regulation” of $V_{c\max}$ has been observed widely in raised-CO₂ experiments: see e.g. Ainsworth and Long, 2005). Low c_a , similarly, should lead to increased $V_{c\max}$. Down-regulation of $V_{c\max}$ at high c_a would tend to reduce the plant demand for N, while increasing A would tend to increase it. Allocation of carbon to fine roots is increased at high c_i , suggesting an adaptive response to an overall increased N demand (e.g. Palmroth et al., 2006). Provided that N demands are met, increased c_a should lead to increased NPP, and reduced c_a should lead to reduced NPP, although changing allocation patterns might limit the magnitude of this response.

The asymptotic nature of the relation between A and c_i , combined with the conservatism of c_i/c_a , implies that g should decline with increasing c_a . This stomatal response to CO₂ has been observed in many species. It could allow water conservation, further increasing photosynthesis in seasons and climates where soil moisture is limiting. Similarly, g should increase with declining c_a . Leaf area index (LAI) under changing CO₂ concentrations is therefore subject to several competing effects. With increasing c_a , increasing A should promote increased LAI, and increasing g might be compensated by increased LAI; but increasing below-ground allocation would reduce LAI. A survey of experimental results by Cowling and Field (2003) indicated that LAI generally declines as CO₂ decreases below present values, while at higher CO₂ levels there is no consistent response of LAI to CO₂.

C₄ plants, with their characteristic CO₂-concentrating leaf anatomy, are believed to have evolved and spread in response to low CO₂ levels (relative to earlier geological epochs) that developed during the Cenozoic (Cerling et al., 1993; Cowling, 2001; Sage, 2004). The rate of C₄ plant photosynthesis can be roughly approximated by disregarding CO₂ effects on A in Eq. (2) and using a reduced value for the quantum efficiency, representing the “cost” of the CO₂-concentrating mechanism. Using the known temperature dependencies of the various photosynthetic parameters, it can be shown that there is a crossover temperature above which C₄ plants can fix carbon at a faster rate than C₃ plants (Ehleringer et al., 1997). Below this temperature, C₄ plants fix carbon at a slower rate than C₃ plants. The crossover temperature increases with increasing CO₂ concentration. Thus, other things being equal, we would expect C₄ plants to be more competitive relative to C₃ plants at low CO₂ (Cole and Monger, 1994; Ehleringer et al., 1997; Collatz et al., 1998). In today’s world, by contrast, C₃ plants should be gaining ground. A widespread trend towards an increase of (C₃) tree cover at the expense of (C₄) grasses has indeed been observed in tropical savannas, and may be an effect of increasing CO₂ concentration (Bond and Midgley, 2000; Eamus and Palmer, 2007). However, other factors including climate change and grazing intensity have been advanced as alternatives (e.g. Archer et al., 1995). This debate continues,

while contemporary observations seem unable to resolve it.

Past environments offer a variety of scenarios involving large and long-lasting CO₂ changes. Although CO₂ changes are inevitably accompanied by climate changes due to the greenhouse effect of CO₂, the involvement of other climate drivers (orbital variations and ice-sheet growth and decay) implies a degree of decoupling between CO₂ and climate which is potentially useful for attempts to attribute causes. Here however we concentrate exclusively on the major shifts in CO₂, climate and vegetation between the last glacial maximum (LGM) and the Holocene, and we use climate and ecosystem modelling results to separate effects of CO₂ from effects of climate on vegetation. In doing so, we briefly survey the history of attempts to depict and model glacial-interglacial variations in the terrestrial biosphere. This endeavour has included some false starts but has now led to a broad consensus, with wide-ranging implications for palaeoclimatology and for carbon cycle science.

3 Glacial-interglacial variations in carbon storage

Shackleton (1977) noted that the calcium carbonate shells of subfossil benthic foraminifera from the last glacial period are light in ¹³C, presumably indicating a change in the stable isotope composition of dissolved inorganic carbon (DIC) in the ocean. His estimate of the $\delta^{13}\text{C}$ offset was -0.7 per mille for the LGM, relative to the Holocene. His hypothesis to explain this offset relies on a transfer of carbon between the land and ocean reservoirs. Terrestrial organic carbon is depleted in ¹³C, so a simple mass balance can be used to infer that terrestrial organic carbon storage was substantially reduced in glacial times.

A glacial-interglacial shift in the $\delta^{13}\text{C}$ of DIC has been confirmed, although its global mean value appears to be smaller, in the range of -0.3 to -0.4 per mille (Currey et al., 1988; Duplessy et al., 1988; Sarnthein et al., 1988; Ku and Luo 1992). Using a canonical value of -0.32 per mille, Bird et al. (1994, 1996) estimated a terrestrial carbon storage reduction of 310–550 PgC at the LGM relative to pre-industrial time. This calculation took account of changes in atmospheric CO₂ content and its $\delta^{13}\text{C}$, as measured in ice cores, and a possible shift in land carbon towards values up to 2 per mille heavier in glacial time (Crowley, 1991). Allowing for further uncertainty in the isotopic shift, Bird et al. (1996) obtained a range of 300–700 PgC. Later estimates have continued to lie within this interval, for example 430–665 PgC (Street-Perrott et al., 1998) and 550–680 PgC (Beerling, 1999), respectively constrained by observations and modelling of the ¹³C content of land carbon at the LGM. Ikeda and Tajika (2003) estimated 630 PgC, by assimilating atmospheric CO₂ concentration and surface- and deep-water ¹³C records into a box model of the ocean carbon cycle. Köhler and Fischer (2004) estimated 600 PgC, using ice-core

measurements of the concentration and $\delta^{13}\text{C}$ of atmospheric CO₂ to constrain a box model of the land carbon cycle.

Various sources of bias in this ocean carbon isotope constraint on terrestrial carbon storage have been suggested, including a dependence of isotopic fractionation during shell formation on carbonate ion concentration (Spero et al., 1997; Pedersen et al., 2003) and degassing of CH₄ clathrates with strongly negative isotopic signatures followed by conversion of the degassed CH₄ to CO₂ (Maslin and Thomas, 2003). We do not attempt a critical analysis of these mechanisms; however, none of them is likely to have a large enough effect to overturn Shackleton's hypothesis, or to require substantial revision of the broad range of estimates of LGM terrestrial carbon storage indicated by Bird et al. (1996). In particular, we note that hypotheses seeking to explain glacial-interglacial CO₂ changes by *increased* carbon storage during glacial times, e.g. buried under ice (Zeng, 2003) or in permafrost soils (Zimov et al., 2006), are manifestly incompatible with the ocean carbon isotope constraint.

Reduced carbon storage on land cannot be accounted for simply by the presence of continental ice sheets, because the area of exposed continental shelf – mainly in the tropics – roughly balanced the land area occupied by ice (Prentice et al., 1993; Montenegro et al., 2006). The explanation requires a change in the distribution of terrestrial biomes, and/or their carbon content. During the early 1990s, many independent estimates of terrestrial carbon storage change between glacial and interglacial regimes were made using “book-keeping” methods that assign *fixed* vegetation and soil carbon storage per unit area to each biome. Such estimates were based either on cartographic reconstructions of past vegetation (e.g. Adams et al., 1990; van Campo et al., 1993; Crowley, 1995; Maslin et al., 1995; Adams and Faure, 1998; and numerous regional studies not cited here), or on palaeoclimate and biogeography modelling using the simple models available at that time (Prentice and Fung, 1990; Friedlingstein, 1992; Prentice, 1993; Prentice et al., 1993; Prentice and Sykes, 1995). All of these estimates should now be rejected, because (a) they overlook variations in carbon storage within biomes, which are large today, and might well vary systematically between climate states; (b) they exclude *a priori* any effect of CO₂ concentration on carbon storage; and (c) the data-based estimates, in particular, offer no consistent way to deal with pollen assemblages that lack modern analogues.

The first modelling studies on this topic produced no reduction in carbon storage at the last glacial maximum (LGM) (Prentice and Fung, 2000), or too small a reduction (e.g. Friedlingstein, 1992; Prentice et al., 1993). This last study invoked peatland development as an additional cause of net postglacial carbon accumulation, but this now seems implausible: there is abundant evidence for glacial-age peats in tropical lowlands, including the exposed continental shelf, which may have stored on the order of 200 PgC that has largely been removed subsequently (Faure et al.,

1996). Esser and Lautenschlager (1994), Peng et al. (1995, 1998) and Friedlingstein et al. (1995) applied early process-based land carbon cycle models to simulate changes in carbon storage since the LGM. These studies noted the potential of physiological CO₂ effects to further reduce carbon storage, and used empirical formulations to demonstrate that the impact could be substantial. Friedlingstein et al. (1995), for example, obtained a total reduction in carbon storage of 470 PgC when the CO₂ effect was included. They also showed that the near-zero carbon change previously simulated by Prentice and Fung (1990) was an artefact, caused by an uncorrected bias in the model used to simulate the LGM climate. Thus, although much was made in older literature of a supposed discrepancy between a small or zero shift in carbon storage (based on models) and a very large shift (based on observations), neither the model-based or the observationally-based estimates can now be considered well-founded.

More recent studies have exploited the advances in palaeoclimate and biosphere modelling made since the 1990s. The current standard approach starts with a palaeoclimate simulation made with a general circulation model (GCM), and applies anomalies (differences in mean monthly climate variables between the simulation and the GCM's control run) to correct a baseline climatology; the altered climate then drives a terrestrial biosphere model (e.g. François et al., 1998). Current models calculate the CO₂ effect based on the Farquhar equations to give changes in photosynthesis, which are propagated through carbon allocation and plant competition algorithms to generate effects at the ecosystem level. Snapshot analyses (e.g. comparisons between the LGM and pre-industrial time slices) can be made using equilibrium models such as CARAIB (Warnant et al., 1994); transient analyses apply dynamic global vegetation models such as LPJ (Sitch et al., 2003). A consensus finding has emerged from these analyses, namely that a carbon shift of approximately the right magnitude *can* be reproduced – but *only* if physiologically mediated effect of CO₂ are included (François et al., 1998, 1999; Otto et al., 2002; Kaplan et al., 2002). These recent analyses have shown consistently that the carbon storage reduction (LGM minus pre-industrial Holocene) with the CO₂ effect “turned off” either is too small, or in some cases even has the wrong sign, i.e. the terrestrial biosphere is modelled to have slightly (<100 PgC) greater carbon storage at the LGM than during the Holocene. The result of François et al. (1998) is typical: producing a carbon storage reduction of 610 PgC when the physiological effect of CO₂ is included, but only 160 PgC when it is not.

There is a simple reason why climate change alone is not sufficient to account for the glacial-interglacial change in terrestrial carbon storage. Other things being equal, the (dominant) soil component of terrestrial carbon storage increases as global temperatures decline, due to slow decomposition of soil organic matter. This explains, for example, why the highest soil carbon storage today occurs in the boreal zone

and not in the tropics. This response is steeper than the positive response of NPP to warming, over a wide range of temperatures. It is a key component of the feedback mechanism believed to be responsible for the small reduction in atmospheric CO₂ content during the Little Ice Age (Joos et al., 2004a; Cox and Jones, 2008). Gerber et al.'s (2003) equilibrium sensitivity analysis with the LPJ model suggested that global cooling to LGM levels would have had a minor impact on total terrestrial carbon storage, whereas the CO₂ change would have reduced terrestrial carbon storage substantially. Kaplan et al. (2002) used LPJ to perform transient simulations of land carbon storage changes since the LGM. They obtained an increase of 820 PgC after the LGM, mainly due to the CO₂ effect. Without the CO₂ effect, the simulated increase was only 210 PgC (Joos et al., 2004b). The increase implies a net extraction of carbon from the ocean to build biospheric carbon on land. This in turn triggered the carbonate compensation mechanism in the ocean, and if the larger figure for post-LGM carbon storage increase is accepted, this mechanism accounts for the greater part of the observed rise in atmospheric CO₂ concentration during the pre-industrial Holocene (Joos et al., 2004b).

The carbon isotope palaeorecord of deep ocean water as preserved in benthic foraminiferal shells, combined with process-based modelling studies to separate the climate and CO₂ effects, thus contains two important messages for contemporary biogeochemistry. (1) The 100 ppm increase in CO₂ concentration from the last glacial period to the Holocene had a major, long-lasting effect on NPP and carbon storage. (2) The approximate magnitude of this effect can be predicted (within the uncertainties of the models and the ocean carbon isotope constraint), but only by models that propagate the physiological effect of CO₂ on photosynthesis into NPP. The earlier proposal by Prentice and Sarnthein (1993) – that climate-induced biome shifts alone might be sufficient to explain glacial-interglacial changes in carbon storage – can no longer be supported. The available evidence on glacial-interglacial changes in terrestrial carbon cycling indicates an important role for physiological effects of CO₂.

4 Biome shifts

The reconstruction of glacial-interglacial changes in terrestrial carbon storage is indirect and therefore subject to rather large uncertainties, as discussed above. The reconstruction of biome shifts is more directly linked to the extremely rich set of observations in the form of pollen and plant macrofossil records from terrestrial sediments. Here, too, current evidence supports a major role for changes in CO₂. Although climate change can certainly influence biome distribution, physiological CO₂ effects modify the growth and competition of different plant functional types (PFTs) and thereby are expected to influence vegetation composition, LAI, structure and biome boundaries (Cowling, 1999, 2004; Bond et al., 2003; Cowling and Shin, 2006).

Jolly et al. (1997) used BIOME3, a process-based coupled biogeochemistry-biogeography model (Haxeltine and Prentice 1996b), to show that CO₂ changes could profoundly affect montane vegetation zonation in the African tropics. BIOME3 is a forerunner of LPJ that lacks only the transient vegetation dynamics which LPJ simulates; it mimics the response of LAI and NPP of different PFTs to climate and CO₂, and competition among PFTs. Jolly et al. (1997) were the first to use a process-based model to analyse the effects of changing CO₂ concentration on ecosystem composition and structure in a palaeoecological context. Their analysis indicated that the large elevational extension of the heath belt on East African mountains was a predictable consequence of the low CO₂ concentration in glacial time. Indirect support for this finding came from ¹³C measurements on leaf waxes preserved in the sediments of a high-elevation lake in the region, which indicated a marked shift towards C₄ plant dominance during the last glacial period (Street-Perrott et al., 1997; Huang et al., 1999). Boom et al. (2002) produced similar results for South America, and used BIOME3 to derive a function relating C₄ plant abundance (as indicated by leaf-wax ¹³C measurements) to temperature and CO₂ concentration which they then inverted to yield a proxy CO₂ record that is broadly consistent with ice-core measurements – a further, indirect confirmation of the role of CO₂ in controlling C₃/C₄ plant competition over glacial-interglacial cycles.

Some early discussions had assumed that effects of glacial CO₂ concentration would be greater at higher elevations, because of low atmospheric pressure (implying a low partial pressure of CO₂ for the same concentration). However the elevation effect also lowers the partial pressure of O₂, which competes with CO₂ at the Rubisco reaction sites; this effect counters the hypothesized effect of a low partial pressure of CO₂ at high elevations (Terashima et al., 1995). In fact, the effects are expected a priori to be greater in warmer climates because the O₂ competition effect is stronger at high temperatures, as reflected in the temperature dependence of the photosynthetic parameters (Cowling, 1999a). Indeed there is abundant evidence in pollen and carbon isotope records from tropical lowland regions for shifts away from forest, toward C₄ dominated vegetation, during glacial times. This evidence comes principally from records of the $\delta^{13}\text{C}$ changes in lake sediments (e.g. Talbot and Johanessen, 1992; Giresse et al. 1994), which can be related to changes in the relative abundance of C₃ and C₄ plants. Modelling with BIOME3 has also indicated consequences for the structure of tropical forests ecosystems which would be largely “silent” in terms of the palaeorecord, yet could be profoundly significant for biogeography (Cowling et al., 2001).

Harrison and Prentice (2004) quantified CO₂ effects at a global scale, based on the BIOME 6000 synthesis, which compiled mid-Holocene and LGM pollen records worldwide and assigned a biome to each record using a standardized method (Prentice et al., 2000). The effect of LGM climate was accounted for by using *all* of the available GCM

experiments from the Palaeoclimate Modelling Intercomparison Project (PMIP) to drive BIOME3. The results were unambiguous. Whichever GCM was used to simulate the LGM climate, the extent of simulated global forest reduction fell short of that observed when CO₂ effects were neglected; but became closer to observations when these effects were included. The influence of CO₂ was largest and most consistent in the tropics, but not confined there: the same effect was seen in the northern and southern extratropics as well. Thus finding is consistent with that of Cowling (1999b), who had also used BIOME3 to show that the pattern of LGM vegetation in eastern North America can be explained satisfactorily only through consideration of reduced water use efficiency (*A/g*) by C₃ plants in low CO₂, favouring more drought-tolerant plant types, as well as climate change; a point also taken up by Loehle (2007).

The conclusion from these studies is that physiological CO₂ effects, as simulated by models based on the fundamentals of photosynthesis and propagated into the simulation of LAI and NPP of different PFTs, are essential in order to fully account for global shifts in forest cover, and probably also to explain a wider range of changes in the relative abundances of PFTs, between glacial and interglacial regimes.

5 Climate reconstruction

Until recently, methods to reconstruct past climates from palaeovegetation data were all statistical, based on the assumption that the climate controls on plant distribution are invariant. These methods broadly fall into two families: those based on some form of regression, and those based on modern analogues – either using a direct search among a set of analogues, or using response surfaces to fit the empirical relationship between the abundances of pollen taxa and climate variables (see e.g. Brewer et al., 2008). It has occasionally been noted that physiologically mediated CO₂ effects could compromise climate reconstructions made by such methods (e.g. Idso, 1989; Cowling and Sykes 1999), but this observation had no impact on research practice until Guiot et al. (2000) developed a novel approach to palaeoclimate reconstruction, based on the numerical inversion of BIOME3.

In inversion-based palaeoclimate reconstruction, a climate change (between the past time under consideration and recent times) is selected using a search algorithm that seeks to maximize goodness of fit between the palaeodata and simulated ecosystem composition (in terms of simulated abundances or productivity of PFTs). A major advantage of using inversion is that it allows the CO₂ level to be accounted for, as it can be prescribed to the model independently of the palaeovegetation data. Guiot et al. (2000) found that prescribing the correct (low) CO₂ made a substantial difference to LGM climate reconstructions. A key finding was that when low CO₂ was prescribed for the LGM, reconstructed winter con-

ditions in the Mediterranean region became (a) *warmer* than in earlier, analogue-based reconstructions, and (b) systematically closer to the predictions made by climate models for the LGM (Ramstein et al., 2007). This result is all the more remarkable because BIOME3 does not model any direct effect of CO₂ on plants' low-temperature tolerance. However, low atmospheric CO₂ implies both reduced NPP (so that the distribution of trees towards climates offering low potential production becomes more restricted) and increased water use per unit of NPP, reinforcing this restriction. As a consequence, steppe vegetation can expand under low CO₂ at the expense of forest. The earlier, analogue-based methods has selected modern analogues for the glacial steppe in central Asia in climates with very cold winters and short growing seasons. Low CO₂, however, permitted the occurrence of steppe vegetation under milder conditions. An expanded set of analogues produced milder reconstructed winters than the original set, but could not produce consistency with palaeoclimate model results. This case study illustrates a relatively little-discussed problem with analogue methods. Although the "no-analogue" problem (fossil pollen assemblages for which similar modern pollen assemblages cannot be found) is well known, there is also potentially a "wrong-analogue" problem whereby the method of modern analogues selects similar pollen assemblages that actually originated in very different physical environments. The Mediterranean case study shows how this problem can be alleviated through the inversion of process-based models. The inversion method has been applied in three continents (Wu et al., 2007a, b; Guiot et al., 2008).

The use of inverse modelling to reconstruct past climates has further advantages that are beginning to be explored, using BIOME3 and most recently its successor, BIOME4 (Kapan et al., 2003). Inverse modelling provides a natural way to incorporate additional observational constraints, such as palaeo ¹³C information (e.g. Hatté and Guiot, 2005; Rousseau et al., 2006; Hatté et al., 2009; Guiot et al., 2009). It makes it straightforward to incorporate additional external forcing of vegetation changes, such as insolation changes caused by orbital variations, and by the differences in latitude between locations at which particular vegetation types occurred during glacial versus interglacial climates; these differences may have implications for plant productivity and water use (Kaplan et al., 2003). The involvement of a process-based model should also allow the use of a data-assimilation approach to the reconstruction of ecosystem properties that palaeodata do not directly record, such as NPP and carbon storage (Wu et al., 2009). Finally, a recent development of the inversion approach builds on a version of the LPJ model to allow time-dependent climate reconstruction taking account temporal lags in the response of vegetation to climate (Guiot et al., 2009). What began as a solution to a specific problem in palaeoclimate reconstruction may turn out to be a tool with a wide field of application in palaeoclimatic analysis.

6 Conclusions

Despite persistent controversies about the contemporary and future effects of rising CO₂, surprisingly few attempts have been made to use palaeorecords to help resolve them. We have summarized evidence based on a model-assisted interpretation of the palaeorecord, which supports the idea that physiological effects do scale up to ecosystem effects, through changes in primary production and through competition between plants with different photosynthetic pathways.

This palaeoperspective has practical implications for modelling of the contemporary carbon cycle. Atmospheric O₂ and ¹³CO₂ concentration measurements show that the land biosphere has been taking up a part of the CO₂ emitted by human activities during recent decades (Prentice et al., 2001; Denman et al., 2007). The land biosphere, in other words, is a net sink for CO₂ due to some process which outweighs the CO₂ release due to land-use change. Process-based models consistently identify this process as a consequence of rising CO₂ concentration, acting through the physiological effect of CO₂ on photosynthesis (McGuire et al., 2001). Without this, models would predict a higher rate of atmospheric CO₂ increase than is observed. Models also predict that this uptake will increase while CO₂ continues to rise, as expected during this century, although it will eventually decline again due to the asymptotic nature of equation (3) and competing effects of warming on the terrestrial carbon balance (Cramer et al., 2001). The palaeorecord suggests that the assumptions underlying existing models regarding CO₂ effects are broadly correct. We do not find support for the opinion (e.g. Körner, 2000) that other constraints effectively eliminate the ecosystem-level effects of changing CO₂ concentration on carbon storage over long time scales. The palaeorecord also supports the attribution of increases in the woody component of tropical savannas to physiological effects of rising CO₂, although this does not rule out a contribution of other factors such as land-use change.

Our findings further imply that for palaeoclimate reconstruction involving periods with substantially different CO₂ levels, inversion of process-based models is likely to yield more realistic results than statistical modelling that excludes physiological effects of CO₂. Recent advances in inverse vegetation modelling offer a promising way forward for the integration of biophysical process understanding into palaeoclimate analysis.

7 Epilogue

Dominique Jolly made pioneering contributions to Quaternary palaeoecology, especially of Africa. He was closely involved in the development of the data analysis technique called “biomization” which made the global BIOME 6000 project possible, and he developed a vision of how modelling and data analysis could work together to achieve new insights about the past. He also produced the first

global-scale simulations of the LGM world that took low CO₂ into account, using an early version of BIOME3. These results were showcased in Berrien Moore III’s plenary presentation at the first International Geosphere-Biosphere Programme Congress in 1996, and presented as an example of how different disciplines of global change science could productively collaborate, and of the power of the new process-based approaches to terrestrial biosphere modelling. We have dealt here with a few of the themes to which Dominique contributed important results and insights. We dedicate this article to the memory of an inspiring colleague and friend.

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